Dynamics of temperate forests: An intoroduction

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DYNAMICS OF TEMPERATE FORESTS: AN INTRODUCTION

The current issue of Folia Geobotanica includes papers on the dynamics of temperate forests, as presented at the 43rd Symposium of the International Association for Vegetation Science, held in Nagano, Japan, in August 2000. Forests are astonishingly complex systems. Their dynamics is often on scales long enough to exceed human lifespans and may be on scales comparable to Holocene climate change. Each of the major climatic zones (tropical, temperate and boreal/austral) has forests that are characterized by a specific set of features: physiological adaptations, the suite of plant life forms that constitutes them, and the processes that drive the forest dynamics. While the dynamics of temperate forests was studied earlier (e.g. CLEMENTS 1916, KNAPP 1974), much interest has recently been devoted also to the dynamics of boreal (e.g. BLACK & BLISS 1978, ENGELMARK et al. 1993) and tropical forests (e.g. WHITMORE 1989, HUBBELL et al. 1999).

The temperate zone and higher latitudes differ from the tropics by the occurrence of freezing temperatures, even at low elevation, and from the higher boreal (or austral) and polar latitudes by a rather warm summertime period. The characteristic feature of temperate forests is, thus, their adaptation to frost – without the long, severe cold and marginal summer warmth of the higher boreal (or austral) and polar latitudes. Temperate-zone plants, including forest trees, are distinctly not tropical or even subtropical in that they have, *inter alia*, adaptations for bud protection during the cold season and well developed mechanisms for winter dormancy, thus avoiding damage due to cold temperatures. Temperate-zone plants also often have some degree of genetically based seasonal programming, which may involve such phenomena as obligate deciduousness, often shorter growing-season requirements, in some cases shorter life cycles, and lower temperature optima for photosynthesis. Another set of features distinguishes temperate forests from boreal (austral) forests: temperate-zone trees generally require growing seasons of at least four months; they require soil that is unfrozen during the growing season, at least to more than just a few centimeters; and they usually do not tolerate the severe cold (< -40 °C) that many boreal and polar plants routinely survive. Succession in temperate forests involves many tradeoffs and biotic interactions, more than just the dominance by physical constraints that characterizes boreal forests. Temperate floras are also much larger than boreal and polar floras.

Apart from these essentially physiological adaptations, temperate forests also differ from boreal/austral and tropical forests in their dynamics. While natural regeneration in all kinds of forests depends on the death of old trees and establishment of seedlings and saplings, the temporal and particularly spatial scale of these processes differs markedly in tropical, temperate and boreal forests. First, tropical and temperate forests differ from boreal forests in their disturbance regimes. In temperate and tropical forests, the predominant gap size is that created by the falling of single or a few canopy trees. In boreal forests, on the other hand, disturbances tend to cover larger areas, such as by blowdown or fire, due partly to the dominance of boreal forests by conifers (e.g. BERGERON et al. 1998). This kind of dynamics is found, in temperate regions, only in rather special habitats, such as in some riverine forests (Sakio et al., this volume).

For temperate forests it was LEIBUNDGUT (1959) who introduced the conceptual model that forests consist of stands of limited area (usually less than 1/2 ha), each representing a developmental phase: regeneration, optimum, or dying phase. According to this concept, temperate forests represent mosaics of patches of different ages. REMMERT (1991), generalizing a concept of AUBREVILLE (1936) developed for West African forests, introduced the "mosaic-cycle concept of ecosystems": i.e. the idea that a forest represents a mosaic of different developmental phases (like Leibundgut) but also that each phase is (or can be) dominated by different species, such that the mosaic cycle is also a (tree) species replacement cycle. Indeed it is possible to find vegetation stands that develop according to that model (e.g. a mopane forest/grass steppe cycle in southern Africa, see REMMERT 1991). In nearly natural temperate forests without fire as a disturbance factor, however, such a tree-species replacement cycle cannot be found. In such forests, in contrast, the climax tree species start to regenerate the destroyed tree layer immediately after the disturbance (e.g. windthrow).

Dynamic features of temperate forests, such as competition, gap dynamics, regeneration patterns, and succession, are the main topic treated in the papers in this special issue. A first group of papers treats features of forest gap dynamics. Regeneration and recovery dynamics are considered further by Yamashita et al. in typhoon-damaged *Fagus* forests of southwestern Japan, and by Fischer et al. (both this volume) in mainly coniferous forests recovering from windthrows in central Europe. Competition for light, dispersal methods and limitations, and seed sources play major roles in these cases. Long-term species coexistence is a direct outcome of general features of forest gap dynamics and gap-phase recruitment, as shown by Busing & Brokaw, using non-spatial and spatial recruitment models. Tropical forests have many more species than do temperate and boreal forests. A species-rich system may include more interactions between plants and animals, such as pollination and seed dispersal, than does a poorer system. Although it might be difficult to say whether it is the cause or the result, forests with many species tend to be maintained by chance more than forests with only a few species (Busing & Brokaw, this volume).

Several other case studies demonstrate the role of specific features and tradeoffs of individual species in species coexistence. Co-existence of three major canopy tree species in riparian forests in Japan is shown to result from tradeoffs in reproductive characteristics and the kinds of disturbance sites that can be invaded (Sakio et al.). Long-term persistence of *Pseudotsuga menziesii* in old-growth forests of northern Pacific North America is shown to result from rapid colonization followed by maintenance of emergent status over long periods of time, a successful sort of "long-lived pioneer" strategy (Ishii & Ford). Tang & Ohsawa show that a Tertiary relict tree, *Davidia involucrata*, has been able to persist and maintain forest stands due to its strong sprouting ability on screes too unstable for other trees. Specific traits of single species may also have ecosystem-wide consequences: primary succession of warm-temperate forest on Miyake-jima (Japan) is faster than in some other volcanic areas, due mainly to the nitrogen-fixing abilities of one colonizing species, shrubby *Alnus sieboldiana* (Kamijo et al.).

Links between climatic constraints and forest dynamics are the subject of two other papers. Plant life form and leaf characteristics are shown by Hildebrandt-Vogel to play a major role in the composition and structure, as well as dynamics, of forests in southern Chile. Finally, new successions and other shifts in forest dynamics are suggested by Walther, due to relaxing of some climatic constraints under the current global warming trend. Spread and increasing competitiveness of evergreen broad-leaved woody species in southern Switzerland, putatively due to warming, is documented from a vegetation sampling programme.

These studies illustrate the especially dynamic nature of temperate forests and the complexity of the mechanisms that may be involved in their regeneration, growth and maturation. Temperate forests are a limited, but important and renewable natural resource: for example for production of timber and wood, protection against soil erosion, as reservoirs of high-quality drinking water, as CO_2 sinks, as sources of biodiversity, and as places of recreation and inspiration. Sustainable management of forests is thus of central importance for humankind. Only if we are very familiar with the processes driving natural forests can we derive methods of sustainable, nearly natural forest management.

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Elgene O. Box[1], Tohru Nakashizuka[2] & Anton Fischer[3]

1) University of Georgia, Geography Department, Athens, Georgia 30602-2502, USA; e-mail boxeo@uga.edu
2) Kyoto University, Center for Ecological Research, Kamitanakami, Hirano-cho, Otsu, Shiga 520-2113, Japan; e-mail toron@ecology.kyoto-u.ac.jp
3) Geobotany, Department of Ecology & School of Forest Science and Resource Management, Center of Life and Food Science TUM, Am Hochanger 13, D-85354 Freising, Germany; e-mail a.fischer@wzw.tum.de